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EVOLUTIONARY HISTORY AND TAXONOMY OF RED ALGAE

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1. Evolutionary Relationship of Red Algae

The red algae (Rhodophyta) form a distinct photosynthetic eukaryotic lineage that consists of around 6,000 species including unicellular to large multicellular taxa (<http://www.algaebase.org/>). The red algae are unique among eukaryotes in lacking both flagella and centrioles during their entire life cycle (Gabrielson et al., 1990; Graham and Wilcox, 2000). Pit connections, pit plugs, and a triphasic life cycle that are mostly found in the Florideophyceae are also distinguishing characters of the red algae. The photosynthetic organelle (plastid) of red algae is bounded by two membranes and contains chlorophyll-*a*, phycocyanin, and phycoerythrin as photosynthetic pigments. These pigment complexes, organized in phycobilisomes, are located on the surface of unstacked thylakoid membranes to capture light energy. As a storage product, the red algae produce granulated floridean starch in the cytoplasm that is different from green algal starch. In addition to these unique features, the monophyly of red algae is strongly supported by nuclear, plastid, and mitochondrial gene trees (Freshwater et al., 1994; Ragan et al., 1994; Van de Peer and De Wachter, 1997; Burger et al., 1999; Yoon et al., 2002b, 2004).

1.1. ORIGIN OF THE RED ALGAL PLASTID AND ITS RELATIONSHIP TO OTHER PLANTAE

It is generally agreed that the red algal plastid originated via primary endosymbiosis. Under this scenario, a photosynthetic cyanobacterium was captured by a heterotrophic protist and the prokaryote was eventually transformed into a plastid. This protistan chimera was an evolutionary success story and gave rise to the three major photosynthetic lineages, i.e., the red, green (including land plants), and glaucophyte algae (Bhattacharya and Medlin, 1995; Delwiche et al., 1995; McFadden, 1999; Bhattacharya et al., 2004; Rodriguez-Ezpeleta et al., 2005;

Hackett et al., 2007a). The kingdom Plantae was established to include these three primary plastid-containing groups that all contain a double-membrane bound photosynthetic organelle that lies free in the cytosol (Cavalier-Smith, 1998). Plantae monophyly is generally recovered when inferring trees with plastid genes (Yoon et al., 2002b, 2004), nuclear genes that encode plastid targeted proteins (Li et al., 2006; Nosenko et al., 2006), and some nuclear gene data (Moreira et al., 2000; Rodriguez-Ezpeleta et al., 2005 [for counter-arguments to Plantae monophyly, see Stiller et al., 2001; Nozaki et al., 2003; Stiller and Harrell, 2005]). The strongest support for Plantae monophyly comes from a 143-gene phylogeny that had however limited taxon sampling (Rodriguez-Ezpeleta et al., 2005), and a 16-gene tree with 46 taxa that included all of the eukaryotic supergroups (Hackett et al., 2007a).

In addition to phylogenetic evidence, Plantae monophyly is supported by shared components of the plastid machinery. For example, the evolutionary history of plastid targeted metabolite translocators in red and green algae (including land plants) suggests a common ancestry of these taxa. These data show that a single gene recruitment event occurred in the ancestral alga followed by duplications and diversification of gene functions that are unique to red and green algae (Weber et al., 2006). These steps were critical for plastid establishment because the plastid translocators connect the biochemistry of the host and organelle to facilitate a regulated flow of metabolites. A similar piece of evidence is provided by the finding of over 55 genes of chlamydial origin in Plantae, many of which are shared by red, green, and glaucophyte algae (Huang and Gogarten, 2007; Moustafa et al., 2008). These genes were recruited from environmental Chlamydiae early in Plantae evolution and have been maintained by algae and plants over the ensuing 1 billion years because of the key functions they provide to plastid and other host-derived functions. The set of plastid targeted translocators and Chlamydiae genes shared uniquely by red and green algae (final assessment of the glaucophyte component awaits completion of the nuclear genome sequence of *Cyanophora paradoxa*; D. Bhattacharya and J. Boore, unpublished data) provides overwhelming evidence that these taxa shared a single common ancestor in which these genetic innovations were established. Finally, Plantae also contain a unique, shared protein import system that is embedded in their organelle membranes (i.e., TOC-TIC translocons, [McFadden and van Dooren, 2004; Reumann et al., 2005]) that also supports a single origin of these taxa. Given that Plantae monophyly is now all but proven, a final piece of data that was recently published demonstrates that within this supergroup, the glaucophytes are the earliest diverging algal lineage. Reyes-Prieto and Bhattacharya (2007) used a concatenated data set of 19 conserved nuclear-encoded plastid targeted proteins to provide robust phylogenetic support for the “glaucophytes first” hypothesis. This result clarifies a long-standing issue in Plantae evolution that was not adequately resolved using plastid gene/genome data and nuclear genes of nonplastid function (e.g., Nozaki et al., 2003; Rodriguez-Ezpeleta et al., 2005; Yoon et al., 2005).

1.2. RED ALGAL FOSSILS AND LINEAGE DIVERGENCE TIMES

There are only a handful of reported unicellular microfossils. Because of their simple morphology and absence of distinguishable characters to suggest a specific affinity, microfossils are generally recognized as cyanobacteria, although some may be of eukaryotic derivation. For example, the unicellular fossils with a mucilage sheath from the 1,900-million-year-old (Ma) Gunflint Formation (Ontario, Canada), *Eosphaera tyleri* are likely to be red algae (Barghoorn and Tyler, 1965; Tappan, 1976); however, this suggestion is still hotly debated. Branched microfossils, acritarchs, were reported from the 1,450 Ma Roper Group, Australia (Javaux et al., 2001). Acritarchs may be fungi, red algae, or of unknown affinity; however, it is generally agreed that these fossils were most likely to have been marine eukaryotic algae (Butterfield, 2005; Porter, 2006).

Besides these controversial microfossils, there are two taxonomically unambiguous remains that may provide a key timeline for red algal evolution. *Bangiomorpha pubescens* is a multicellular filamentous fossil that was found in the 1,200 Ma Hunting Formation from Somerset Island, Canada (Butterfield, 2000). These fossils are almost completely preserved and regarded as the oldest taxonomically resolved eukaryotic fossil (Fig. 1). *B. pubescens* is very similar to modern *Bangia* species in cell division pattern, holdfast shape, and gross morphology. In addition to multicellularity, the fossils have spores/gametes that putatively represent differentiation due to sexual reproduction. Therefore, these fossils may indicate the occurrence of a major red algal radiation in the Mesoproterozoic. The other clear examples of red algal fossils are florideophycean algae (*Thallophyca* and *Paramecia*) from the ca. 600 Ma Doushantuo Formation in China (Xiao et al., 1998, 2004). The Doushantuo pseudoparenchymatous thalli are likely to be extinct coralline algae that contain carposporophytes, suggesting the presence of a triphasic life cycle that is typical for extant Florideophyceae. Because the coralline algae are not an early diverging lineage in the Florideophyceae (Saunders and Kraft, 1997), the diversification of Florideophyceae (e.g., Hildenbrandiophycidae is the earliest diverging florideophycean lineage) must have occurred prior to the age of Doushantuo (600 Ma).

On the basis of six reliable fossil data points including *Bangiomorpha* and the Doushantuo algae, Yoon et al. (2004) estimated an evolutionary timeline for photosynthetic eukaryotes using a six-gene data set and “relaxed” clock molecular phylogenetic methods. These authors suggested ca. 1,500 Ma for divergence of the red and green algal lineages, 1,370 Ma for the Cyanidiophyceae split, ca. 1,300 Ma for the secondary endosymbiosis that eventually gave rise to the plastid in chromalveolate lineages, and ca. 800 Ma for the divergence of the Florideophyceae from the Bangiales. They postulated that the noncyanidiophycean lineages (i.e., five major unresolved red algal groups) radiated around 1,200 Ma over a relatively short evolutionary time period (Yoon et al., 2004). A widely cited molecular clock analysis that contradicts a Mesoproterozoic origin of red algae was done by Douzery et al. (2004) who suggested that Plantae originated between 892 and 1,162 Ma, which is about 500 million years later than the estimate made by Yoon et al. (2004)

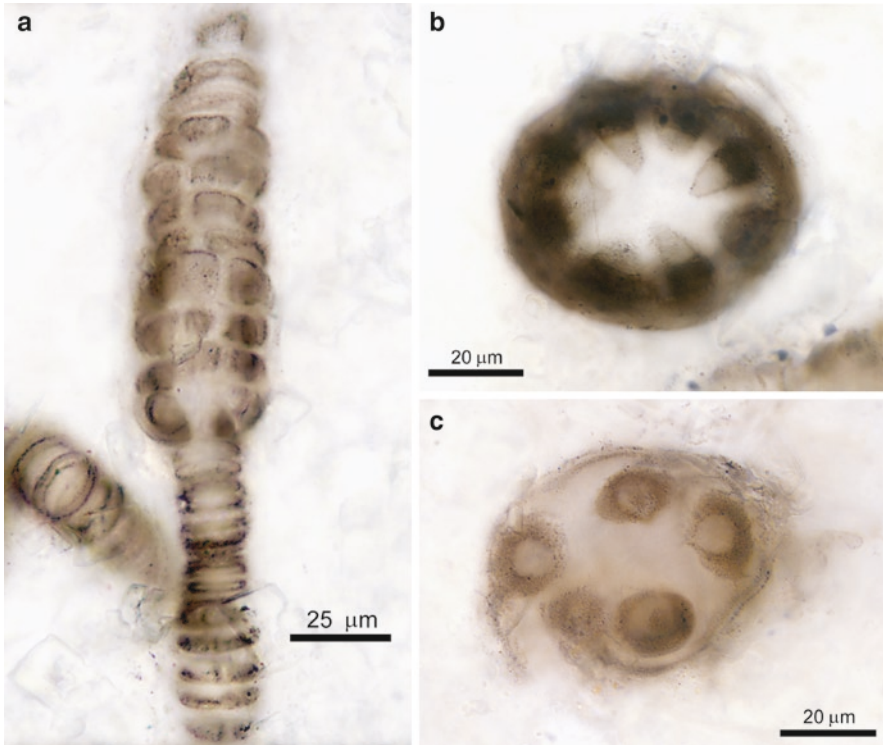


Figure 1. *Bangiomorpha pubescens* fossils from the ca. 1,200 Ma Hunting Formation, Somerset Island, arctic Canada. (a) Mature thallus showing both uniseriate and multiserial portions of a filament; (b) transverse cross-section of a multiserial filament showing eight radially arranged wedge-shaped cells, exactly comparable with the longitudinal intercalary division in extant *Bangia*; (c) transverse cross-section of a four-part multiserial filament, which has differentiated to form spheroidal spores that is comparable with the asexual monospores of extant *Bangia* (courtesy of N. J. Butterfield).

and a subsequent analysis by Hackett et al. (2007b). It should be noted that the Douzery et al. (2004) date is derived from a large 129-protein data set, but with limited taxon sampling. If true, this work is clearly inconsistent with the broadly accepted fossil data cited above by proposing a 928 Ma divergence for the red algae and 872 Ma split for stramenopiles. The reasons for these inconsistencies remain unclear and await future in-depth analyses that incorporate genome data from a broader diversity of eukaryotes.

2. Classification of the Rhodophyta

A classification system for a group of organisms should reflect its phylogeny. A reliable phylogeny ideally uses both broad taxon sampling and sufficient phylogenetic information (Yoon et al., 2006).

The Rhodophyta is one of the three phyla in the kingdom Plantae. Red algae have traditionally been classified into two classes Bangiophyceae and Florideophyceae (Gabrielson et al., 1985), or two subclasses Bangiophycidae and Florideophycidae of the class Rhodophyceae (Dixon, 1973). This morphology-based taxonomy was challenged with the onset of numerical cladistics and molecular systematics. Garbary and colleagues suggested paraphyly of the Bangiophyceae *sensu lato* based on cladistic analysis of morphological characters (Gabrielson et al., 1985; Gabrielson et al., 1990; Garbary and Gabrielson, 1990). Molecular systematic studies (Freshwater et al., 1994; Ragan et al., 1994; Saunders and Kraft, 1997; Oliveira and Bhattacharya, 2000; Müller et al., 2001) using nuclear or plastid genes (16S SSU, 18S SSU, and *rbcL*) confirmed that Bangiophyceae *sensu lato* is not a monophyletic clade and reported that the Porphyridiales are paraphyletic, including at least three independent lineages (Porphyridiales-1, -2, and -3). The monophyly of the Bangiales and the Florideophyceae was also proposed using these data (e.g., Oliveira and Bhattacharya, 2000; Müller et al., 2001). Recent multigene phylogenetic analyses (albeit with a narrow sampling of taxa) found that the Cyanidiophyceae is the earliest diverging red algal lineage (Yoon et al., 2002b, 2004). In summary, both single and multigene approaches, with or without a broad taxon sampling, identify the major lineages within the red algae but fail to resolve their interrelationships.

Saunders and Hommersand (2004) revised the current classification system and proposed a new taxonomic scheme. In addition to the phylum Rhodophyta, they suggested the new phylum Cyanidiophyta with a single class Cyanidiophyceae under the new subkingdom Rhodoplantae. A three-subphylum (Rhodellophytina, Metarhodophytina, and Eurhodophytina) with four-class (Rhodellophyceae, Compsopogonophyceae, Bangiophyceae, and Florideophyceae) system was proposed for the phylum Rhodophyta. It is noteworthy that they attempted to incorporate red algal molecular phylogenies and ultrastructural characters (i.e., Golgi–ER association) into their taxonomic system that together provided a useful definition of classes in the red algae. They also established the subphylum Eurhodophytina to define the strongly supported monophyletic group of class Bangiophyceae and Florideophyceae. However, they defined the paraphyletic class Rhodellophyceae *classis nova* that includes three independent lineages (i.e., Porphyridiales, Stylonematales, and Porphyridiales-1, *sensu* Müller et al., 2001).

Yoon et al. (2006) conducted a comprehensive molecular systematic analysis using a broad taxon sampling with multigene analyses (Table 1). They included most of the phylogenetic lineages of Bangiophyceae *sensu lato* (25 genera, 48 taxa) to represent red algal diversity. On the basis of the finding of seven well-supported lineages, they proposed a new classification system of the Rhodophyta that contains two new subphyla, the Cyanidiophytina with a single class, the Cyanidiophyceae, and the Rhodophytina with six classes, the Bangiophyceae, Compsopogonophyceae, Florideophyceae, Porphyridiophyceae *classis nova*, Rhodellophyceae, and Stylonematophyceae *classis nova*. They also described a new order, Rhodellales, and a new family, Rhodellaceae. Although they used

Table 1. Current taxonomic system of the red algae according to Yoon et al. (2006).

Kingdom Plantae Haeckel
Phylum Rhodophyta Wettstein
Subphylum Cyanidiophytina Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Cyanidiophyceae Merola, Castaldo, De Luca, Gambardella, Musacchio et Taddei
Order Cyanidiales Christensen
Subphylum Rhodophytina Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Bangiophyceae Wettstein
Order Bangiales Nägeli
Class Compsopogonophyceae Saunders et Hommersand
Order Compsopogonales Schmitz in Engler et Prantl
Order Erythropeltidales Garbary, Hansen, et Scagel
Order Rhodochaetales Bessey
Class Florideophyceae Cronquist
Subclass Hildenbrandiophycidae Saunders et Hommersand
Order Hildenbrandiales
Subclass Nemaliophycidae Christensen
Order Acrochaetiales, Balbianiales, Balliales, Batrachospermales, Colaconematales,
Corallinales, Nemaliales, Palmariales, Rhodogorgonales, Thoreales
Subclass Ahnfeltiophycidae Saunders et Hommersand
Order Ahnfeltiales
Subclass Rhodymeniophycidae Saunders et Hommersand
Order Bonnemaisoniales, Ceramiales, Gelidiales, Gigartinales, Gracilariales,
Halymeniales, Nemastomatales, Plocamiales, Rhodymeniales
Class Porphyridiophyceae Yoon, Müller, Sheath, Ott, et Bhattacharya
Order Porphyridiales Kylin ex Skuja
Class Rhodellophyceae Cavalier-Smith
Order Rhodellales Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Stylonematophyceae Yoon, Müller, Sheath, Ott, et Bhattacharya
Order Stylonematales Drew

multigene data sets (i.e., seven-genes 2,564 amino acid sequences, nine-genes 10,463 bp), the multigene phylogenies still failed to resolve interrelationships between the noncyanidiophycean lineages (Fig. 2). This may not primarily reflect insufficient phylogenetic information, but rather a rapid radiation of the red algal lineages over a relatively short evolutionary timeframe. Therefore, the seven-class system may be a reasonable classification for the red algae.

3. Seven Classes of Rhodophyta

3.1. CLASS CYANIDIOPHYCEAE

The Cyanidiophyceae is an asexual, unicellular red algal class that belongs to the subphylum Cyanidiophytina. These taxa thrive in acidic and high temperature conditions around hot springs or acidic sulfur fumes (Pinto et al., 2003).

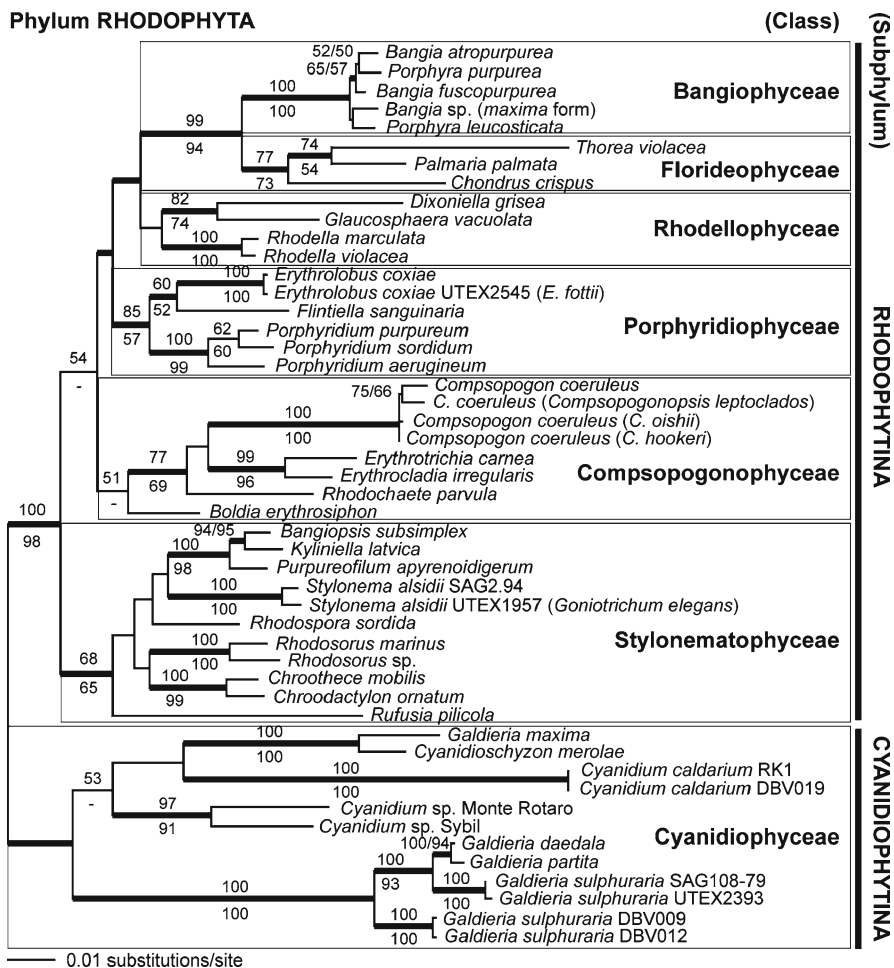


Figure 2. Maximum likelihood (ML) phylogeny of the red algae using the combined plastid protein sequences of *psaA* and *rbcL*. The results of a ML bootstrap analysis are shown above the branches, whereas the values below the branches result from a maximum parsimony bootstrap analysis. The thick branches indicate clades to the right with a greater-than-95% Bayesian posterior probability.

The Golgi apparatus in these species associates with the ER. The Cyanidiophyceae is a well-supported monophyletic group that diverged earliest within red algae around 1,370 Ma prior to the chromalveolate red algal secondary endosymbiosis (i.e., according to Yoon et al., 2004). Traditionally, the Cyanidiophyceae was classified into one order Cyanidiales, two families Cyanidiaceae and Galdieriaceae, and three genera *Cyanidium* (1 sp.), *Cyanidioschyzon* (1 sp.), and *Galdieria* (5 spp.). Because of their simple morphology, only seven species are recognized to date (Merola et al., 1981; Sentsova, 1991; Ott and Seckbach, 1994; Albertano et al., 2000; Pinto et al., 2003, 2007). It is, however, now clear that the diversity of the

Cyanidiophyceae was underestimated. Ciniglia et al. (2004) used an environmental PCR survey to find the hidden biodiversity among Cyanidiophyceae and suggested six putative family-level taxa within the cyanidiophycean lineage; the *Galdieria* lineage (as *Galdieria*-A), the endolithic *Galdieria* (*Galdieria*-B), the mesophilic *Cyanidium* lineage, the *Cyanidium* lineage, the *Cyanidioschyzon* lineage, and the *G. maxima* lineage (Fig. 2), which is essentially consistent with other molecular phylogenetic studies (Gross et al. 2001; Yoon et al., 2002a, 2006; Pinto et al., 2003). For example, the endolithic *Galdieria*-B was recently established as the new species *Galdieria phlegrea* by Pinto et al. (2007). On the basis of molecular phylogenetic analyses (Ciniglia et al., 2004), they conducted additional eco-physiological studies to characterize this new species. *G. maxima* and *Cyanidioschyzon merolae* showed a close sister group relationship; however, *G. maxima* is very different from *C. merolae* with regard to many morphological features (e.g., spherical vs. ellipsoidal cell shape, thick cell wall vs. lack of cell wall, facultative heterotroph vs. obligate autotroph, endospore vs. binary fission). It is clear that the current taxonomic scheme does not reflect the underlying phylogenetic relationships. Therefore, there needs to be a thorough revision of the classification system of the Cyanidiophyceae at the higher level (i.e., family level) as well as a comprehensive sampling of potentially new taxa (e.g., environmental PCR survey) to characterize the hidden biodiversity in this group.

3.2. CLASS BANGIOPHYCEAE

Bangiophyceae is a group of red algae that has simple unbranched filaments or a leaf-shaped thallus. The monophyly of the Bangiophyceae is supported by most molecular phylogenetic studies (Oliveira and Bhattacharya, 2000; Müller et al., 2001; Broom et al., 2004; Yoon et al., 2006). The Bangiophyceae grows in both marine and freshwater habitats. A biphasic life cycle is common in the group that includes macroscopic gametophyte and microscopic conchocelis phases. The monophyly of the Bangiophyceae and Florideophyceae is supported by morphological as well as molecular data (see below). *Bangiomorpha* and *Porphyra* fossils are found in deposits of ages 1,200 Ma and 600 Ma, respectively (see above, Butterfield et al., 1988; Xiao et al., 1998; Butterfield, 2000). The Bangiophyceae includes one order Bangiales, one family Bangiaceae, and six genera *Bangia*, *Bangiadulcis*, *Dione*, *Minerva*, *Porphyra*, and *Pseudobangia*. Around 130 species are reported from the six genera, but the majority of species belong to *Bangia* (10 sp.) and *Porphyra* (117 sp.; <http://www.algaebase.org/>). Broom et al. (2004) collected 123 samples of *Bangia*, which had been recognized as ten species and reported significant hidden genetic diversity within this genus. Continuing efforts have erected the monotypic genera *Bangiadulcis*, *Dione*, *Minerva*, and *Pseudobangia* (Müller et al., 2005; Nelson et al., 2005; Nelson, 2007). However, it is obvious that a comprehensive taxonomic study is required for this group as well to uncover their “real” diversity.

3.3. CLASS FLORIDEOPHYCEAE

The monophyly of the Bangiophyceae and Florideophyceae is supported not only by molecular analyses but also by features of the reproductive cells, the association of the Golgi apparatus with ER/mitochondria, the presence of pit connections, and the presence of group I introns (Gabrielson et al., 1985, 1990; Freshwater et al., 1994; Ragan et al., 1994; Oliveira and Bhattacharya, 2000; Müller et al., 2001; Yoon et al., 2002b, 2004, 2006). Regarding, the close relationship between Bangiophyceae and Florideophyceae, Saunders and Hommersand (2004) suggested the subphylum Eurhodophytina to include these taxa. The class Floridiophyceae appears to have diverged from an ancestor of bangiophycean and florideophycean alga around 800 Ma (Yoon et al., 2004) and is the most taxonomically diverse of all red algal groups, including around 5,800 species. The Florideophyceae is one of the most successful algal groups in marine environments, perhaps because of their specialized life cycles (e.g., triphasic life cycle; gametophyte, carposporophyte, and tetrasporophyte phases). These red algae possess unique and distinctive female reproductive structures that are often used as taxonomic markers with respect to postzygotic development. On the basis of morphological and molecular phylogenetic data (Pueschel and Cole, 1982; Maggs and Pueschel, 1989; Harper and Saunders, 2002; Huisman et al., 2003; Saunders et al., 2004), the Florideophyceae is classified into four subclasses Hildenbrandiophycidae, Nemaliophycidae, Ahnfeltiophycidae, and Rhodymeniophycidae. Although internal relationships within these groups are still unclear, the four subclass system provides an overall view of florideophycean classification. For a detailed review of the Florideophyceae, see Saunders and Hommersand (2004).

3.4 CLASS COMPSOPOGONOPHYCEAE

The Compsopogonophyceae consists of one freshwater order Compsopogonales with two families Boldiaceae and Compsopogonaceae, and two marine orders Erythropeltidales and Rhodochaetales. Fourteen genera have been reported in this class (*Compsopogon*, *Boldia*, *Chlidophyllon*, *Erythrocladia*, *Erythropeltis*, *Erythrotrichia*, *Membranella*, *Porphyropsis*, *Porphyrostromium*, *Pulvinaster*, *Pyrophyllon*, *Rhodochaete*, *Sahlingia*, *Smithora*). All of these species are multicellular; *Erythrotrichia* is filamentous, *Smithora* and *Chlidophyllon* are parenchymatous blades, and *Boldia* is a single-cell-thick tubular form that is 20–75 cm in length. The monophyly of this group is supported by nuclear SSU rDNA and a plastid multigene analysis that show a sister relationship of Erythropeltidales and Rhodochaetales (Rintoul et al., 1999; Zuccarello et al., 2000; Müller, et al., 2001; Yoon et al., 2002b, 2006). This recently established class (Saunders and Hommersand, 2004) is characterized by having a Golgi–ER association, and floridoside as the low-molecular-weight carbohydrates (LMWC; Broadwater and Scott, 1994; Karsten et al., 2003). This class is also the only group outside the Bangiophyceae

and Florideophyceae in which sex (a complete life cycle or putative sexual structures) has been well documented (Magne, 1960, 1990) or proposed (Hawkes, 1988; Nelson et al., 2003). The divergence of this class parallel to the Bangiophyceae/Florideophyceae clade indicates that sex was established in the Rhodophyta before the putative fossil evidence provided by *Bangiomorpha*.

3.5. CLASS PORPHYRIDIOPHYCEAE

The Porphyridiophyceae includes one order Porphyridiales, one family Porphyridiaceae, and three unicellular genera, *Erythrolobus*, *Flintiella*, and *Porphyridium*. This unicellular red algal group contains a single branched or stellate plastid with the presense of a group II intron (genic position 1219) in the plastid-encoded *psaA* gene from *Flintiella* (Table 2). It was reported that *Flintiella* and *Porphyridium* have a Golgi association with ER/mitochondria (Scott et al., 1992) and possess floridoside as a LMWC (Karsten et al., 2003).

Table 2. The seven classes and all recognized genera of the Rhodophyta (excluding Florideophyceae) and some of their diagnostic characters (ER = endoplasmic reticulum; ER/M = ER-mitochondrion association; Nu = nucleus).

Class	Genus	Golgi association	Low-molecular-weight carbohydrate (LMWC)	Other characters
Cyanidiophyceae	<i>Cyanidium</i>	ER		
	<i>Cyanidioschyzon</i>			
Bangiophyceae	<i>Galdieria</i>	ER		
	<i>Bangia</i>		Floridoside, isofloridoside	
	<i>Bangiadulcis</i>			
	<i>Dione</i>			
	<i>Minerva</i>			
	<i>Porphyra</i>		Floridoside, isofloridoside	
	<i>Pseudobangia</i>			
Florideophyceae	Hundreds of genera			
Compsopogonophyceae	<i>Compsopogon</i>	ER	Floridoside	
	<i>Boldia</i>	ER	Floridoside	
	<i>Chlidophyllon</i>			
	<i>Erythrocladia</i>		Floridoside	
	<i>Erythropeltis</i>			
	<i>Erythrotrichia</i>		Floridoside	
	<i>Membranella</i>			
	<i>Porphyropsis</i>		Floridoside	
	<i>Porphyrostromium</i>			
	<i>Pulvinaster</i>	ER	Floridoside	

(continued)

Table 2. (continued)

Class	Genus	Golgi association	Low-molecular-weight carbohydrate (LMWC)	Other characters
Porphyridiophyceae	<i>Pyrophyllon</i>	ER/M	Floridoside, digeneaside	
	<i>Rhodochaete</i>			
	<i>Sahlingia</i>			
	<i>Smithora</i>			
	<i>Porphyridium</i>			
Rhodellophyceae	<i>Erythrolobus</i>	ER	Floridoside	Intron (1,219/psaA)
	<i>Flintiella</i>			
	<i>Rhodella</i>			
	<i>Dixoniella</i>			
Stylonematophyceae	<i>Glaucosphaera</i>	Nu	Mannitol	
	<i>Stylonema</i>	ER	Sorbitol, digeneaside	intron (229/psaA)
	<i>Bangiopsis</i>	ER	Sorbitol, digeneaside	Intron (229/psaA)
	<i>Chroodactylon</i>	ER	Sorbitol	Intron (229/psaA)
	<i>Chroothece</i>			Intron (229/psaA)
	<i>Colacodictyon</i>			
	<i>Empselium</i>			
	<i>Goniotrichopsis</i>			
	<i>Kylinella</i>			
	<i>Neevea</i>			
	<i>Purpureofilum</i>		Sorbitol, digeneaside	Intron (229/psaA)
	<i>Rhodaphanes</i>		Sorbitol, digeneaside, trehalose	
	<i>Rhodorus</i>		Sorbitol, digeneaside	Intron (229/psaA)
	<i>Rhodospira</i>		Sorbitol, dulcitol	Intron (229/psaA)
	<i>Rufusia</i>		Floridoside	Intron (229/psaA)

3.6. CLASS RHODELLOPHYCEAE

The class Rhodellophyceae was proposed by Cavalier-Smith (1998) and modified/retained by Saunders and Hommersand (2004); however, both definitions were not natural. Yoon et al. (2006) have revised the class as a group that includes unicellular red algae, *Dixoniella grisea*, *Glaucosphaera vacuolata*, *Rhodella violacea*, and *R. maculata*. The monophyly of the Rhodellophyceae is supported by multigene (Yoon et al., 2006) and 18S rDNA trees (Müller et al., 2001). This group contains mannitol as a LMWC (Karsten et al., 2003). Within the lineage, *D. grisea* and *G. vacuolata* are separated from two *Rhodella* species. Ultrastructural characters

support the relationship between *Dixoniella* and *Glaucosphaera*, which have a Golgi–Nuclear association with the presence of peripheral thylakoids, whereas *Rhodella* has a Golgi–ER association with the absence of peripheral thylakoids (Scott et al., 1992). Furthermore, group II introns were found at genic position 91 in the *psaA* gene only in two *Rhodella* species (*R. violacea*, *R. maculata*). Therefore, it may be possible to classify the two groups into separate orders or families. Additional work may show that more genera or families need to be established to encompass this diversity.

3.7. CLASS STYLONEMATOPHYCEAE

The Stylonematophyceae was proposed by Yoon et al. (2006) based on multigene phylogenetic analyses. This class includes pseudofilamentous or unicellular taxa with thick mucilaginous walls and cells lacking pit plugs. With the single order Stylonematales, the single family Stylonemataceae contains 14 genera (*Bangiopsis*, *Chroodactylon*, *Chroothece*, *Colacodictyon*, *Empselium*, *Goniotrichopsis*, *Kylinella*, *Neevea*, *Purpureofilum*, *Rhodaphanes*, *Rhodorus*, *Rhodospora*, *Rufusia*, and *Stylonema*) that have been reported mostly from marine habitats. Most genera have cells with a single stellate plastid with a pyrenoid. A Golgi–ER association with digeneaside and sorbitol as a LMWCs are diagnostic characters for this group (Broadwater and Scott, 1994; Karsten et al., 2003), although digeneaside is missing in *Chroodactylon* and dulcitol is present in *Rhodospora*. A group II intron was found at genic position 229 in the *psaA* gene from most of the species (Table 2). Recently, West and colleagues isolated two new genera *Rhodaphanes* and *Purpureofilum* belonging to this class (West et al., 2005, 2007). Most of the pseudofilamentous species in this group are found as epiphytes, and it is expected that new taxa will continue to be discovered.

4. Summary

The red algae are one of the most distinct eukaryotic groups. This photosynthetic lineage acquired its plastid from a cyanobacterium through primary endosymbiosis ca. 1,600 Ma, and then became a plastid donor to the chromalveolates through secondary endosymbiosis. This latter lineage is the most morphologically and taxonomically diverse eukaryotic group known. Therefore, the red algae have contributed significantly to eukaryote evolution. The classification of the Rhodophyta in a two-class system (i.e., Bangiophyceae and Florideophyceae) has been accepted by most red algal taxonomists for several decades. This morphological character-based system was, however, challenged by recent molecular systematic studies. It has been suggested that the Bangiophyceae *sensu lato* are paraphyletic and the Bangiales and Florideophyceae are monophyletic. Saunders and Hommersand (2004) suggested a two-phylum and five-class system for the red algae; however, it retains the paraphyletic class Rhodellophyceae. In contrast, Yoon et al. (2006)

conducted a molecular systematic analysis using multigene data with a broad taxon sampling and suggested two-subphyla and seven-class system that reflects phylogenetic relationships.

In this review, we hope that the reader appreciates that there remains significant hidden biodiversity among red algae. Novel taxa are being added to the red algae (e.g., Cyanidiophyceae, Bangiophyceae) and will significantly increase the number of species. This growth in biodiversity needs of course to be reflected in future taxonomic schemes. We also suggest that single gene approaches may not be sufficient to resolve interrelationships among higher-level groups of red algae. Multigene or genomic methods with a broad taxon sampling strategy (i.e., including all genera from at least the non-Florideophyceae) should allow us to resolve interrelationships between classes that will be a guide to establish a natural classification system for the red algae.

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